

# Plant-endophyte symbiosis, an ecological perspective

Zahoor Ahmed Wani · Nasheeman Ashraf ·  
Tabasum Mohiuddin · Syed Riyaz-Ul-Hassan

Received: 13 January 2015 / Revised: 13 February 2015 / Accepted: 15 February 2015 / Published online: 10 March 2015  
© Springer-Verlag Berlin Heidelberg 2015

**Abstract** Endophytism is the phenomenon of mutualistic association of a plant with a microorganism wherein the microbe lives within the tissues of the plant without causing any symptoms of disease. In addition to being a treasured biological resource, endophytes play diverse indispensable functions in nature for plant growth, development, stress tolerance, and adaptation. Our understanding of endophytism and its ecological aspects are overtly limited, and we have only recently started to appreciate its essence. Endophytes may impact plant biology through the production of diverse chemical entities including, but not limited to, plant growth hormones and by modulating the gene expression of defense and other secondary metabolic pathways of the host. Studies have shown differential recruitment of endophytes in endophytic populations of plants growing in the same locations, indicating host specificity and that endophytes evolve in a coordinated fashion with the host plants. Endophytic technology can be employed for the efficient production of agricultural and economically important plants and plant products. The rational application of endophytes to manipulate the microbiota, intimately asso-

ciated with plants, can help in enhancement of production of agricultural produce, increased production of key metabolites in medicinal and aromatic plants, as well as adaptation to new bio-geographic regions through tolerance to various biotic and abiotic conditions. However, the potential of endophytic biology can be judiciously harnessed only when we obtain insight into the molecular mechanism of this unique mutualistic relationship. In this paper, we present a discussion on endophytes, endophytism, their significance, and diverse functions in nature as unraveled by the latest research to understand this universal natural phenomenon.

**Keywords** Endophytes · Endophytism · Multitrophic interaction · Phytoremediation · Plant adaptation · Systems biology approach

## Introduction

Endophytic biology is pursued in research with multitude of objectives that can be broadly classified into two categories—*bioprospecting* and *plant-microbe symbiosis* (Fig. 1). The bioprospecting aspect of endophytism has been extensively reviewed (Aly et al. 2011; Porrás-Alfaro and Bayman 2011; Mousa and Raizada 2013; Chen et al. 2014; Brader et al. 2014; Strobel 2015). However, the other aspect, i.e., plant-microbe *symbiosis*, at molecular level, has been poorly understood (Rodríguez and Roossinck 2012; Saikkonen et al. 1998; Ryan et al. 2008). Plant-microbe interactions are ubiquitous and diverse in nature (Redman et al. 2002; Kuldau and Bacon 2008; Mitter et al. 2013). In fact, each plant is a complex community, rather than a single organism, owing to its engagement in diverse heterospecific associations (Kiers and Denison 2008; Rodríguez et al. 2009; Rey and Schornack 2013). The complex interplay of diverse array of microbial communities with the host plant affects its ecophysiology such

---

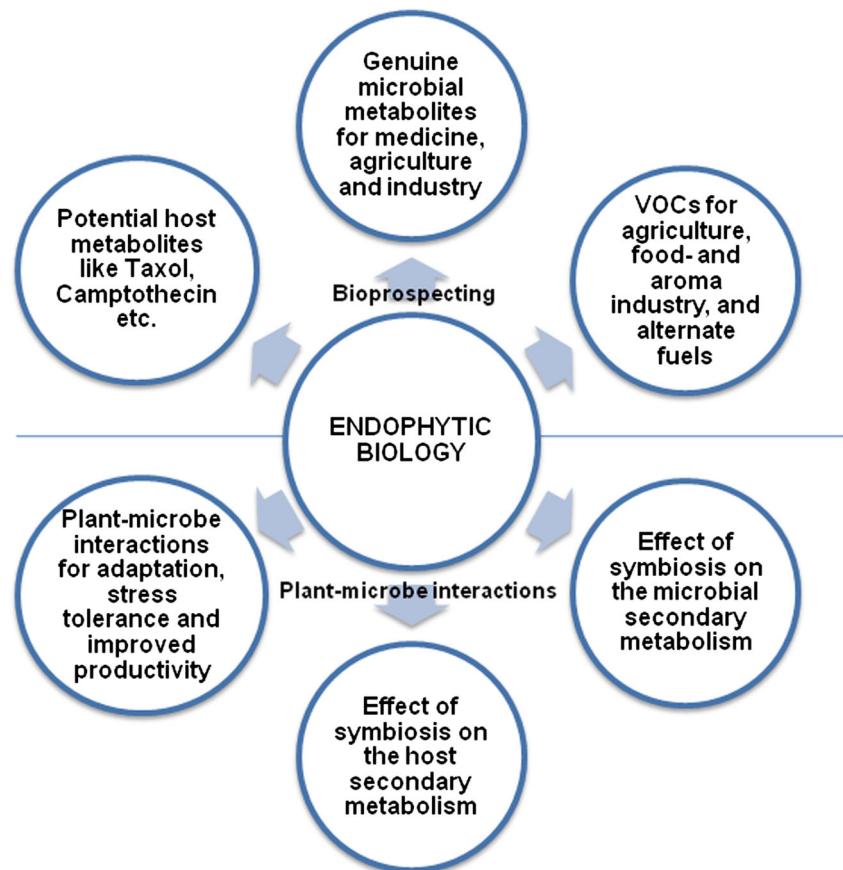
Z. A. Wani · S. Riyaz-Ul-Hassan  
Microbial Biotechnology Division, CSIR-Indian Institute of  
Integrative Medicine, Canal Road, Jammu Tawi 180 001, India

N. Ashraf · T. Mohiuddin  
Plant Biotechnology Division, CSIR-Indian Institute of Integrative  
Medicine, Sanat Nagar, Srinagar 190 005, India

Z. A. Wani · N. Ashraf · T. Mohiuddin · S. Riyaz-Ul-Hassan (✉)  
Academy of Scientific and Innovative Research, CSIR-Indian  
Institute of Integrative Medicine, Canal Road, Jammu Tawi 180 001,  
India  
e-mail: srhassan@iiim.ac.in

S. Riyaz-Ul-Hassan  
e-mail: riyaz.andrabi@gmail.com

**Fig. 1** Endophytic biology is studied with the aim of bioprospecting for genuine microbial products, potential host metabolites, and industrially important volatile organic compounds (VOCs) or to understand the principles of endophytism and its consequences on the secondary metabolism of the partners as well as adaptation of the plant host to biotic and abiotic stress conditions



as plant nutrition, growth rate, resistance to biotic and abiotic stress conditions, as well as plant survival and distribution (Reinhold-Hurek and Hurek 2011; Singh et al. 2011; Iqbal et al. 2013). Owing to the fact that the association of plants with microbes dates back to more than 400 million years ago, along with the modern scientific reports of these associations, it can be stated with certainty that the presence of symbiotic microorganisms inside the plant tissues “must be considered to be the rule, rather than the exception” (Strobel et al. 2004; Albrechtsen et al. 2010; Partida-Martínez and Heil 2011).

Endophytism as a natural phenomenon is a question of history, and its origin probably dates back to the existence of plants on the planet earth (Redecker et al. 2000), but its advancement as a discipline of science began in 1886 when De Barry put forth the concept of “endophyte.” However, this discipline of science did not receive much attention until the recent recognition of their pharmaceutical and ecological significance (Gunatilaka 2006). Since then, endophytes have created immense scientific curiosity pertaining to their biology, evolution, ecology, and applications. The aim of this paper is to present a general description of endophytes in the light of recent scientific reports with an emphasis on its general classification, interaction with plants, communication between endophytes and host plants, and differential recruitment of endophytes. Furthermore, the importance of endophyte

technology is also discussed with examples of their potential application in agriculture, drug discovery, and bioremediation.

### Classification of endophytes

Previously, fungal endophytes were categorized into two general groups viz. clavicipitaceous and non-clavicipitaceous based on their taxonomy, host specificity, evolution, and ecological functions. However, Rodriguez et al. (2009) described four distinct functional groups based on six criteria viz., host range, tissue(s) colonized, in planta colonization pattern, in planta biodiversity levels, mechanism of transmission between host generations, and ecological functions. Clavicipitaceous endophytes are referred to as class 1, and non-clavicipitaceous endophytes are further classified into three distinct functional groups as class 2, class 3, and class 4 (Rodriguez et al. 2009).

However, endophytes comprise different groups of microorganisms, and there is a wide diversity of nonfungal endophytes associated with almost every plant. The endophytic microorganisms can be bacteria, fungi, actinomycetes, or viruses (Stepniewska and Kuzniar 2013; Bao and Roossinck 2013) while they express a variety of symbiotic lifestyle ranging from parasitism to mutualism (Redman et al. 2001; Schulz

and Boyle 2005) depending on the plant host genotype and/or environmental conditions. Endophytes are classified into two general categories, systemic/true endophytes and transient/nonsystemic endophytes, based on their taxonomy, functional diversity, biology, and mode of transmission (Table 1).

The concept of systemic/true endophytes was put forth by Mostert et al. (2000). Systemic endophytes can be defined as the organisms that inhabit the plant organization, share a symbiotic relationship with the host, and do not produce any visible symptoms of disease at any stage. However, the widely accepted definition of Petrini (1991) with a minor modification is valid for the transient endophytes, as the organisms that live within the plant tissues at least for part of their life cycle without producing any apparent disease symptoms in plants under normal conditions but turn pathogenic when host plant is stressed or resource-limited. Systemic endophytes are cocladogenetic, i.e., in different environmental conditions, a given host possesses phylogenetically same endophytes, while as transient endophytes vary both in diversity and abundance with change in environment (Botella and Diez 2011; Higgins et al. 2014). These endophytes, because of coevolutionary selection process, share the metabolic and genetic makeup of the host and are resistant to host metabolites and/or defense mechanism (Christensen et al. 2008; Soliman et al. 2013). Systemic endophytes share a symbiotic relationship with the host plant and when grown under axenic conditions may lose their vitality after subculturing. For example, recently, it was found that a camptothecin-producing endophyte, *F. solani* isolated from *C. acuminata* (Kusari et al. 2009), could indigenously produce the precursors of camptothecin. However, a host plant enzyme absent in the fungus, strictosidine synthase, was employed in planta for the key step in producing camptothecin (Kusari et al. 2012). This was the main reason for substantial reduction of camptothecin production on subculturing under axenic conditions. The possible reason for this molecular and metabolic cross talk may be horizontal gene transfer between endophyte and the host plant (Kusari and Spiteller 2012). However, the

association of transient endophytes is short lived and seasonal; therefore, they share only physiological cues, and their diversity varies with change in the host's physiological parameters in relation to varying environmental conditions (Botella and Diez 2011). As systemic endophytes are symbiotically associated with the host plant, their transmission to next generation would be usually vertical, i.e., by means of seeds and/or vegetative propagules, while as the transient endophytes are horizontally transmitted, via spores (Scharndl et al. 1991; Saikkonen et al. 1998; Moricca and Ragazzi 2008).

### Endophytism: a unique interaction between the microbe (endophyte) and the plant

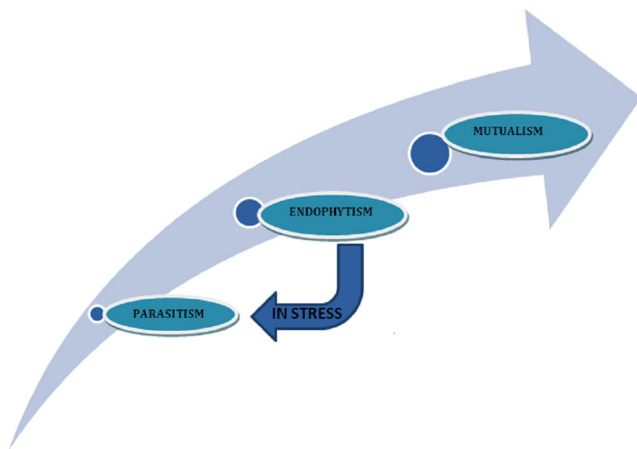
According to the theory of “balanced antagonism” the endophyte-host interactions (endophytism) exhibit great phenotypic plasticity from mutualism to antagonism depending on the biocommunication between endophytes and host plant and environmental conditions (Schulz and Boyle 2005). In widely studied epichloe endophyte association, it has been reported that in some *Epichloe* spp., the onset of flowering in the host plant induces the fungal endophyte to switch from mutualistic asexual life cycle to antagonistic sexual life cycle (Scharndl et al. 2004). Prevailing views contend that fungal endophytes are presumably thought to have evolved from plant pathogenic fungi, as evidenced by some root endophytic fungi that require host cell death for proliferation during the formation of mutualistic symbiosis with the host plants; they remain asymptomatic for many years and only become parasitic when their hosts are stressed (Deshmukh et al. 2006; Kogel et al. 2006). In general, a variety of microbes may enter and become transient endophytes, and those consistently found inside the host tissues for long periods of time and eventually share the physiological and genetic makeup of the host are candidate symbionts or true endophytes (Moricca and Ragazzi 2008; Conn et al. 2008). Recently, it has been reported that the establishment of biotrophic lifestyle

**Table 1** Criteria for classification of endophytes into systemic and nonsystemic endophytes

Criteria	Systemic endophytes	Nonsystemic endophytes
1. Taxonomy	Cocladogenetic species	Varies spatially and temporally
2. Mode of transmission	Usually vertical but in some cases horizontal as well	Horizontal only
3. Life style	Mutualistic	Changes from mutualism to parasitism with change in environment
4. Host defense response	Lack host defense response	Host defense response is active
5. Ecological functions	Beneficial	Beneficial or detrimental depending on the environment, age of the plant, etc.
6. Evolutionary pattern	Coevolved with the host plant	Association with the host is transient and short lived
7. Diversity	Rare	Rich

of endophytes during the colonization of host plants is an important feature of the host endophyte interactions, as it implies a strong genetic and metabolic relief to both the interacting partners. However, the response of long-term association of an endophyte may be mutualistic or antagonistic depending on nutrient availability to the endophytes and metabolic status of the host plant (Eaton et al. 2011; Lahrman et al. 2013). Also, some endophytes produce signals like reactive oxygen species (ROS), which result in switching of endophytism to either antagonism or mutualism in response to some environmental cues (White and Torres 2010). Thus, endophytes, in the earlier stage, are detected as minor pathogens which over a period of time evolve with the host into a benign or mutualistic symbiont with varying degrees of dependence, depending on the cost-benefit analysis of the host-endophyte association (Fig. 2) (Freeman and Rodriguez 1993; Schulz and Boyle 2005; Conn et al. 2008).

The other unique aspect of endophytism is the multitrophic association between different endophytic groups and the host plants. The variegated cross talks between endophytic fungi, endophytic bacteria, endophytic viruses and between these endophytes and the host plants under different biotic and abiotic selection pressures shape the outcome of this cross-kingdom symbiosis (Kusari et al. 2012; Rodriguez and Roossinck 2012). As in case of *Dichanthelium lanuginosum* (host plant) and *Curvularia protuberata* (fungal endophyte) association, the thermotolerance ability in the host plant provided by the endophytic fungal symbiont was because of a double-stranded virus harbored by the fungal endophyte (Márquez et al. 2007; Rodriguez and Roossinck 2012). Therefore, in order to understand the complexity of endophytism, future endophyte research should focus on multitrophic association models with cost-benefit analysis of communications between different interacting partners in a systems biology approach.



**Fig. 2** Evolutionary progression of the host-endophyte relationship

## Mechanism of action of endophytes in the host plant

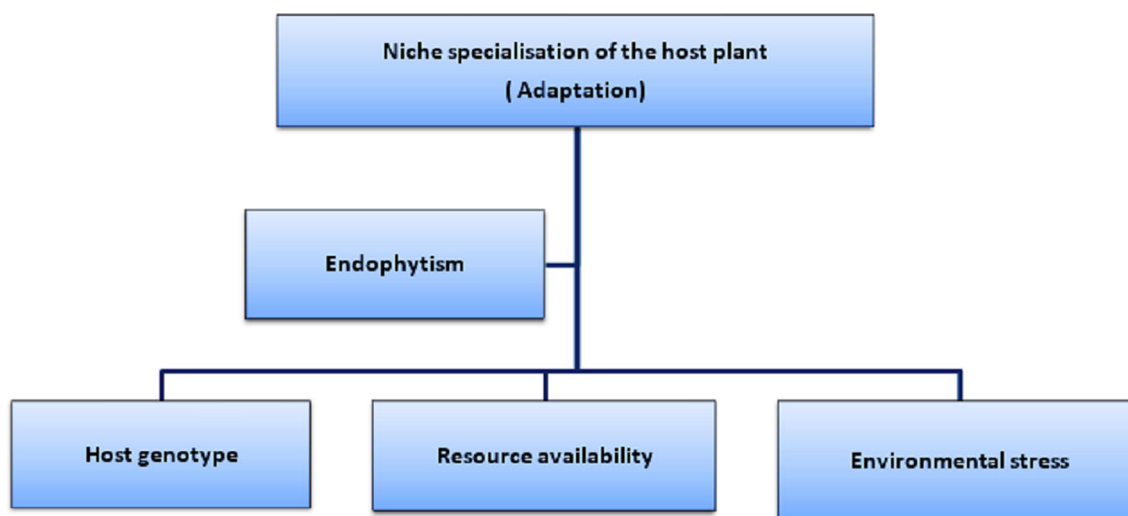
Researchers have endeavored to elucidate the molecular mechanisms underlying the establishment of plant-endophyte association and their responses, but very limited data is available as of now (Sherameti et al. 2005; Mathys et al. 2012; Straub et al. 2013). There are two main reasons for it, one is the complex relationship between the host and the endophyte and the other is that it is not easy to imitate living condition of endophytes in vitro as well as studying the mechanisms in planta. It is generally believed that the endophytic response in plants is largely primed by the plant genotype, endophyte species, and endophyte strain (Gundel et al. 2012; Qawasmeh et al. 2012). Broadly, there are two basic mechanisms, through which endophytes affect their responses in host plants:

1. By producing diverse chemical entities (reactive oxygen species (ROS), phytoalexins, phytohormones, volatile organic compounds (VOCs), toxicants, antibiotics, peptaibols, etc.) (Schirmbock et al. 1994; Griffin et al. 2010; Khan et al. 2012), it has been reported that in some plant lines inoculated with endophytes, there was more growth in the roots, and by far, the most common mechanism that endophytes use to stimulate root growth is through secretion of phytohormones within the plant (Khan et al. 2012; Waqas et al. 2014). Also, endophytic interactions with the host generate reactive oxygen species stimulating antioxidant production in their host plants, which in turn are responsible for protecting the hosts from oxidative stress (Tanaka et al. 2006; White and Torres 2010). Recently, it was reported in *Lolium perenne* that colonization with the endophyte, *Neotyphodium lolii* significantly influenced the phenolic content and antioxidant activity. However, the effect was found to be dependent on the endophytic strain (Qawasmeh et al. 2012). In addition to this, some endophytes manipulate the host plant metabolism by changing the nutrient uptake and nutrient homeostasis (Sherameti et al. 2005; Singh et al. 2013).
2. By altering/inducing gene expression of plants' defense and metabolic pathways (Rosenblueth and Martínez-Romero 2006; Sherameti et al. 2008; Mathys et al. 2012), it is well established that the interaction of microbes with plants can induce both local and systemic alterations in the host (Heil and Bostock 2002; Glazebrook 2005; Ownley et al. 2010). Studies of plant gene expression in response to endophytic colonization reveal that genes for C and N metabolism, and plant growth and plant defense are induced (Elvira-Recuenco and Van Vuurde 2000). Plants can detect the presence of molecules from endophytes through chemoperception systems (Boller 1995). Recognition of endophytes by

the host plants triggers a cascade of signal transduction, which gives rise to a series of plant defense responses similar to plant pathogen interaction, thus leading to a noticeable change in plant metabolic state (Qawasmeh et al. 2012). The endophytic rhizobacteria and actinobacteria have been shown to enhance disease resistance by stimulating the systemic defense pathways (Heil and Bostock 2002; Conn et al. 2008). The systemic acquired resistance (SAR) pathway in the model plant, *Arabidopsis*, is normally activated by biotrophic pathogens either as a part of the hypersensitive response or as a symptom of disease, and the jasmonic acid/ethylene (JA/ET) pathway is triggered by infection with necrotrophic pathogens (Durrant and Dong 2004; Glazebrook 2005). However, the activation of plant defense genes in the absence of a pathogen by endophytic actinobacteria reveals that the latter are detected as “minor” pathogens which do not trigger a full resistance response on their own, because they do not have pathogenic determinants; thus, this may result in more effective priming of the defense response (Conn et al. 2008). Recently, it was reported that an endophytic bacterium *Bacillus thuringiensis* GS1 isolated from *Pteridium aquilinum* induced defense response against *Rhizoctonia solani* KACC 40111 in cucumber plants. The possible mode of action was reported to be the induction of PR proteins and defense-related enzymes by *B. thuringiensis* GS1 against *R. solani* KACC 40111 in cucumber plants (Seo et al. 2012). Though this is some of the basic work done on mechanistic aspect of endophytism, a complete comprehension of this ecological phenomenon can only be obtained by the integration of the “omics” technologies, such as metagenomics, metabolomics, or transcriptomics together with ecogenomics.

### Are endophytes a metabolic drain on plants or an ecological bargain?

Symbiotic plant-fungal interactions are of widespread interest to ecological research as they influence important ecosystem processes including plant productivity, plant diversity, and plant pathogen interactions (Van der Heijden et al. 2006; Rodriguez et al. 2009; Van Bael et al. 2012), as exemplified by the association of endophytic systemic clavicipitaceous fungi with grasses exerting beneficial effects on hosts, through increased resistance to herbivores, pathogens, and drought stresses, which are of great ecological significance (Kuldau and Bacon 2008). Many environmental factors influence the plant-endophyte interactions; however, host plant response to endophyte infection is mainly mediated by the host genotype, endophytic strain, resource availability, and environmental cues (Fig. 3) (Hesse et al. 2003; Malinowski and Belesky 2006; Singh et al. 2011; Qawasmeh et al. 2012). For example, the endophyte interactions in tall fescue develop a low osmotic potential, primarily in young meristematic and elongating leaves, which enable tall fescue to remain stable during drought stress (Elmi and west 1995). Similarly, thermotolerance and salt tolerance is observed in certain plants colonized with endophytes (Redman et al. 2002; Waller et al. 2005). Fungal endophyte colonization significantly affects both primary and secondary metabolism of its host plant, clearly demonstrating the need for wider metabolic studies beyond alkaloid accumulation to understand ecosystem functions of this association (Vandenkoornhuyse et al. 2002; Rudgers et al. 2012). It has been reported that a shift in C to N ratios and in secondary metabolite production due to endophyte colonization are likely to have impacts on herbivore and plant pathogen responses to grasses infected with *Neotyphodium* sp. (Rasmussen et al. 2008). Recent studies have shown that plant



**Fig. 3** Endophytism derived niche specialization of plants leading to their adaptation to varied environmental conditions and bio-geographical regions

microsymbionts may produce a range of different types of metabolites that not only play a role in defense and competition, but also take part in specific interactions and communication with the host plant (Brader et al. 2014). Further, metagenomic studies in rice found that endophytic root bacteria contain several groups of genes involved in motility, plant polymer degradation, iron acquisition (e.g., siderophores), quorum-sensing, and detoxification of reactive oxygen species, indicating that control over those pathways is important for colonization by the root microbiome (Sessitsch et al. 2012). Also, the phenotype and functional traits of most plants in nature are product of the multitrophic interactions of plants with other organisms, mainly microorganisms, sharing the same habitat and resulting in complex and transient metabolic flux across the interacting partners essential for their survival (Kusari et al. 2014). It has also been found that positive effects of the endophyte on plant performance depend on genetic variation in the host and endophyte and on nutrient availability (Cheplick 2007; Gundel et al. 2012). This link between resource availability and beneficial or neutral versus detrimental effects on plant performance suggests a metabolic cost of the endophyte to the host plant (Rasmussen et al. 2008; Lahrmann et al. 2013). Thus, fungal symbionts might be a drain (net cost) on plant metabolism or might upregulate metabolism, but endophyte hosting plants have been reported to have increased tolerance to drought, heat, metal toxicity, low pH, and high salinity, thereby invoking an ecological significance to the plants (Waller et al. 2005; Rodriguez et al. 2008; Singh et al. 2011; Nagabhyru et al. 2013).

### Why is there a differential recruitment of endophytes?

Plants growing in different geographical regions are confronted with different environmental challenges (Arnold 2007). These environmental cues, in combinatorial effect with host genotype, may shape the endophytic diversity harbored by the host plants (Vega et al. 2010). The diversity of endophytes associated with the plants varies not only temporally but spatially as well (Herrera et al. 2010; Ek-Ramos et al. 2013). For instance, studies showed that endophytes may increase in incidence, diversity, and host breadth as a function of latitude (Arnold and Lutzoni 2007). Furthermore, endophyte communities from higher latitudes were characterized by relatively few fungal species representing several classes of Ascomycota, whereas tropical endophyte assemblages were dominated by a small number of classes but a very large number of different endophytic species (Arnold and Lutzoni 2007).

Also, the different plants growing in similar environmental conditions do not harbor same endophytes. It was observed that none of the endophytes isolated from cottonwood were identical to any of the endophytes of willow, even though both

tree species were growing at the same site within a meter of distance from each other (Doty et al. 2009). This differential “recruitment” of endophytes has been noted in other studies of endophytic populations from plants growing in the same location. Ulrich et al. (2008), while studying the diversity of endophytes within four clones of poplar, noted that the four poplar clones harbored four distinct endophytic populations, supporting the hypothesis that plant genotype plays a role in determining which endophyte can colonize the host (Ulrich et al. 2008). A recent metagenomic study of root-associated microbiomes of rice, using plants grown under controlled conditions as well as field cultivation, showed that the composition of the microbial consortia varies with root-associated compartments viz. endosphere (root interior), rhizoplane (root surface), and rhizosphere (soil close to the root surface). Under controlled conditions, microbiome composition varies with soil source and genotype, while as in field conditions, geographical location and cultivation practice were the factors responsible for microbiome variation. This differential recruitment of microbes across the rhizocompartments is a result of active selection of microbial consortia at different steps and each step involving molecular signals (general plant metabolites, cell wall components or membrane proteins, small molecule hormones particularly jasmonic acid, salicylic acid, and ethylene) from the plant. These results suggest that a core microbiota can be recruited from very diverse microbial surroundings, narrowing down both the most relevant community members and pointing to the host detriments controlling the mechanisms of assembly (Lebeis 2014; Edwards et al. 2014).

The above-mentioned findings suggest that the endophytic community of the plants is determined by the combinatorial effect of the host genotype and the environment consistent with a coevolutionary process whereby the endophytes may have evolved in a coordinated fashion with the host plants (Saikkonen et al. 2004; Heath 2010). There is the evidence for multiple horizontal transfers of genes between the symbionts, as an important ecological event that conferred a selective advantage on the interacting partners (Saikkonen et al. 2004). However, the interactions between plant and symbiotic microbial genomes (i.e., intergenomic epistasis, or genotype (G)×genotype (G) interactions) can have important effects on the rate and direction of coevolutionary selection (Wade 2007). Thus, it can be hypothesized that differential recruitment of endophytes in plants is a result of coevolutionary selection process determined by intergenomic interactions of both the interacting partners with environmental conditions acting as a catalyst in this evolutionary selection process. However, the genetic principles governing the differential recruitment of endophytes by a specific host and in a particular environment are poorly understood and need to be deliberated in future.

## Endophytic technology and its ecological implications

The complexity of association of endophytes with its host plant is of great ecological significance owing to their compatibility, ease of reinfection, and pattern of colonization (Backman and Sikora 2008; Sikora et al. 2010). Whenever we think of a microbial infection to plants, symptoms of diseases or detrimental effects come to our mind, but this is not true in case of endophytes. However, research work in this aspect of plant-microbe interactions, with respect to the endophytes, is in infancy, and the molecular mechanism to understand this unique relationship is yet to be explored. Interests are often also dictated by more immediate socioeconomic impulses because microbes are responsible for many plant diseases that cause substantial economic losses in agriculture or have a substantial aesthetic impact. These harmful effects are often manifested directly through pathogen-mediated damage to the plants and a consequent reduction in plant vigor and yield or quality of crops. However, there is a diverse community of microorganisms (endophytes) which interact positively with plants in agricultural systems in relation to their nutrition and ability to resist biotic and abiotic stress and have the potential to be manipulated such that the benefits of their positive effects are harnessed. Endophytes can be genetically engineered, and these engineered endophytes have the potential to provide an alternative to plant transgenic technology by conferring plants a new pathway to benefit from foreign genes (Li et al. 2007). For example, an endophyte *Leifsonia xyli* subsp. *cynodontis*, a xylem inhabiting bacterium, was genetically modified with a gene from *Bacillus thuringiensis*, producing Delta-endotoxin which is active against insects in nature, especially Lepidoptera and Coleoptera. When inoculated in the plant, it secretes the toxin inside the plant tissues protecting it against attacks from the target insects (Fahey et al. 1991; Tikhonovich and Provorov 2009; Porras-Alfaro and Bayman 2011; Selim et al. 2012; Saikkonen et al. 2013). Endophytes are especially interesting for integrative pest management as innovative biological control agents (BCAs) (Scherwinski et al. 2008; Berg 2009; Li et al. 2012). An important advantage of endophytes as BCAs over the conventional BCAs is that they can be applied directly to seeds or seedlings, thereby avoiding treatment to large quantities of soil or large numbers of already established plants. Recently, an *Enterobacter* sp. has been reported as a potent biocontrol agent against *Verticillium dahliae* Kleb, which is the causative agent of verticillium wilt of cotton (Li et al. 2012). Few fungal endophytes are already being produced on large scale as commercial BCAs for example *Trichoderma harzianum*, *Paecilomyces lilacinus*, *Beauveria bassiana*, *Fusarium oxysporum* etc. (Mendoza and Sikora 2009; Sikora et al. 2010). However, so far, single microorganisms have been used as BCAs, and the use of multiple organisms in a consortium imitating the complexity of associations within the plant

system has just begun to be explored (Friesen 2012; Kiers et al. 2013). As the world becomes wary of the ecological damage done by synthetic agrochemicals, endophytes continue for the discovery of powerful, selective, and safe alternatives. The other important aspect of biotechnological implication of endophytes is in phytoremediation process either directly through degradation and/or accumulation of environmental pollutants or indirectly by promoting the growth of plants having the ability of phytoremediation (Stepniewska and Kuzniar 2013). For example, plants inoculated with genetically engineered endophytes were more tolerant to toluene, and they also reduced the transpiration of toluene to the atmosphere (Newman and Reynolds 2005). Some endophytes have been found to help the host plant in nitrogen acquisition, either by tapping atmospheric nitrogen directly (Sherameti et al. 2005) or by translocating the insect-derived nitrogen indirectly (Behie et al. 2012) and thereby may play a larger role in nitrogen cycling. One of the most potential functions of endophytes is the facilitation of nutrient uptake. Some endophytes have been observed to mobilize phosphorous uptake in plants (Yadav et al. 2010), while others have been found to impact the growth and development of the plants by producing useful phytohormones (Khan et al. 2012; Waqas et al. 2014).

Many of the fungal endophytes have been found to produce antimycotic volatile organic compounds (VOCs). VOCs produced by microorganisms are regarded important infochemicals in the biosphere which influence the dynamics of the ecosystem and vice versa (Wheatley 2002). Microbial species produce consistent and reproducible VOC profiles under standard culture conditions (Strobel et al. 2008; Mallette et al. 2012; Riyaz-Ul-Hassan et al. 2012). Several of these endophytes may find applications in agriculture, aroma industry, food processing, and as potential biofuel molecules (Ezra et al. 2004; Strobel et al. 2008; Bitas et al. 2013; Riyaz-Ul-Hassan et al. 2013). Endophytes like *Muscodor* spp. produce bioactive VOCs that inhibit or kill important plant pathogens, thus may be used for mycofumigation, postharvest preservation of agricultural produce, and decontamination of animal waste (Strobel 2006; Bitas et al. 2013). It seems reasonable that the VOC-producing microorganisms may be preferentially establishing symbiotic associations with higher plants as they contribute to the host defense mechanism by inhibiting the plant pathogens. Production of VOCs may also help them to compete with other microbes for space, nutrients, and making associations with plants.

Greater utilization of microorganisms of endophytic origin in agricultural systems could possibly allow reductions in the use of inorganic fertilizers, herbicides, and pesticides with no impact on crop vigor and yield. Thus, in future, endophyte technology holds the key for a potential gateway to sustainable agriculture development.

## Conclusions

The microbiota associated with the plants shape their health, growth, and development as well as their secondary metabolism. Endophytes are most intimately associated with plants, being present inside the plant tissues; thus, they impact the development of the host significantly. Plant-endophyte interactions may be species specific, shaped by the coevolution of both the partners together to impart essential benefits to each other. Recent studies on plant-endophyte mutualism involving “-omics” coupled to the systems biology approaches have started providing insights into different facets of plant-endophyte interactions and the dynamics of multispecies mutualism network with a high level of significance. Endophytes can be explored as a bio-resource for drug discovery in pharmaceutical industries, as plant growth-promoting regulators (PGPRs), bio-control agents (BCAs) for disease and pest management in agricultural industry, and as important technology in environmental remediation. Thus, endophyte research holds a potential gateway for sustainable development provided that we harness their potential in a holistic way.

**Acknowledgments** ZAW and TM are grateful to the Council of Scientific and Industrial Research (CSIR), India, for their respective fellowships. SRH and NA acknowledge the financial support obtained from CSIR 12th FYP projects “PMSI” (BSC0117) and “SIMPLE” (BSC0109) of the Council of Scientific and Industrial Research (CSIR), New Delhi, India. This review paper bears the institutional manuscript number IIIM/1757/2015.

**Conflict of interest** The authors report no declarations of interest.

## References

- Albrechtsen BR, Björkén L, Varad A, Hagner A, Wedin M, Karlsson J, Jansson S (2010) Endophytic fungi in European aspen (*Populus tremula*) leaves—diversity, detection, and a suggested correlation with herbivory resistance. *Fungal Divers* 41:17–28
- Aly AH, Debbab A, Proksch P (2011) Fungal endophytes: unique plant inhabitants with great promises. *Appl Microbiol Biotechnol* 90: 1829–1845
- Arnold AE (2007) Understanding the diversity of foliar fungal endophytes: progress, challenges, and frontiers. *Fungal Biol Rev* 21: 51–66
- Arnold AE, Lutzoni F (2007) Diversity and Host range of foliar fungal endophytes: Are tropical leaves biodiversity hotspots? *Ecology* 88: 541–549
- Backman PA, Sikora RA (2008) Endophytes: An emerging tool for biological control. *Biol Control* 46:1–3
- Bao X, Roossinck MJ (2013) Multiplexed interactions: viruses of endophytic fungi. *Adv Virus Res* 86:37–57
- Behie SW, Zelisko PM, Bidochka MJ (2012) Endophytic insect-parasitic fungi translocate nitrogen directly from insects to plants. *Science* 336:1576–1577
- Berg G (2009) Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. *Appl Microbiol Biotechnol* 84:11–18
- Bitas V, Kim HS, Bennett JW, Kang S (2013) Sniffing on microbes: diverse roles of microbial volatile organic compounds in plant health. *Mol Plant Microbe Interact* 26:835–843
- Boller T (1995) Chemoperception of microbial signals in plant cells. *Annu Rev Plant Physiol Plant Mol Biol* 46:189–214
- Botella L, Diez JJ (2011) Phylogenetic diversity of fungal endophytes in Spanish stands of *Pinus halepensis*. *Fungal Divers* 47:9–18
- Brader G, Compant S, Mitter B, Trognitz F, Sessitsch A (2014) Metabolic potential of endophytic bacteria. *Curr Opin Biotechnol* 27:30–37
- Chen L, Zhang QY, Jia M, Ming QL, Yue W, Rahman K, Qin LP, Han T (2014) Endophytic fungi with antitumor activities: Their occurrence and anticancer compounds. *Crit Rev Microbiol* 24:1–20
- Cheplick GP (2007) Costs of fungal endophyte infection in *Lolium perenne* genotypes from Eurasia and North Africa under extreme resource limitation. *Environ Exp Bot* 60:202–210
- Christensen MJ, Bennett RJ, Ansari HA, Koga H, Johnson RD, Bryan GT, Simpson JP, Koolaard WR, Nickless EM, Voisey CR (2008) Epichloë endophytes grow by intercalary hyphal extension in elongating grass leaves. *Fungal Genet Biol* 45:84–93
- Conn VM, Walker AR, Franco CM (2008) Endophytic actinobacteria induces defense pathways in *Arabidopsis thaliana*. *Mol Plant Microbe Interact* 21:208–218
- Deshmukh S, Hüchelhoven R, Schäfer P, Imani J, Sharma M, Weiss M, Waller F, Kogel KH (2006) The root endophytic fungus *Piriformospora indica* requires host cell death for proliferation during mutualistic symbiosis with barley. *Proc Natl Acad Sci* 103: 18450–18457
- Doty SL, Oakley B, Xin G, Kang JW, Singleton G, Khan Z, Vajzovic A, Staley JT (2009) Diazotrophic endophytes of native black cottonwood and willow. *Symbiosis* 47:23–33
- Durrant WE, Dong X (2004) Systemic acquired resistance. *Annu Rev Phytopathol* 42:185–209
- Eaton CJ, Cox MP, Scott B (2011) What triggers grass endophytes to switch from mutualism to pathogenism? *Plant Sci* 180:190–195
- Edwards J, Johnson C, Santos-Medellin C, Lurie E, Podishetty NK, Bhatnagar S, Eisen JA, Sundaresan V (2014) Structure, variation, and assembly of the root-associated microbiomes of rice. *Proc Natl Acad Sci*. doi:10.1073/pnas.1414592112
- Ek-Ramos MJ, Zhou W, Valencia CU, Antwi JB, Kalns LL, Morgan GD, Kerns DL, Sword GA (2013) Spatial and Temporal Variation in Fungal Endophyte Communities Isolated from Cultivated Cotton (*Gossypium hirsutum*). *PLoS One* 8:e66049
- Elmi AA, West CP (1995) Endophyte infection effects on stomatal conductance, osmotic adjustment and drought recovery of tall fescue. *New Phytol* 131:61–67
- Elvira-Recuenco M, Van Vuurde JW (2000) Natural incidence of endophytic bacteria in pea cultivars under field conditions. *Can J Microbiol* 46:1036–1041
- Ezra D, Hess WH, Strobel GA (2004) New endophytic isolates of *M. albus*, a volatile antibiotic-producing fungus. *Microbiol* 150: 4023–4031
- Fahey JW, Dimock MB, Tomasino SF, Taylor JM, Carlson PS (1991) Genetically engineered endophytes as biocontrol agents: a case study in industry. *Microb Ecol Leaves* 401–411
- Freeman S, Rodriguez RJ (1993) Genetic conversion of a fungal pathogen to a nonpathogenic, endophytic mutualist. *Science* 260:75–78
- Friesen ML (2012) widespread fitness alignment in the legume–rhizobium symbiosis. *New Phytol* 194:1096–1111
- Glazebrook J (2005) Contrasting Mechanisms of Defense against Biotrophic and Necrotrophic Pathogens. *Annu Rev Phytopathol* 43:205–227
- Griffin MA, Spakowicz DJ, Gianoulis TA, Strobel SA (2010) Volatile organic compound production by organisms in the genus *Ascocoryne* and a re-evaluation of myco-diesel production by NRRL 50072. *Microbiol* 156:3814–3829



- Gunatilaka AAL (2006) Natural products from plant-associated microorganisms: distribution, structural diversity, bioactivity, and implication of their occurrence. *J Nat Prod* 69:509–526
- Gundel PE, Martinez-Ghersa MA, Omacini M, Cuyeu R, Pagano E, Rios R, Ghersa CM (2012) Mutualism effectiveness and vertical transmission of symbiotic fungal endophytes in response to host genetic background. *Evol Appl* 5:838–884
- Heath KD (2010) Intergenomic epistasis and co-evolutionary constraint in plants and rhizobia. *Evolution* 64:1446–1458
- Heil M, Bostock RM (2002) Induced systemic resistance (ISR) against pathogens in the context of Induced Plant defences. *Ann Bot* 89: 503–512
- Herrera J, Khidir HH, Eudy DM, Porrás-Alfaro A, Natvig DO, Sinsabaugh RL (2010) Shifting fungal endophyte communities colonize *Bouteloua gracilis*: effect of host tissue and geographical distribution. *Mycologia* 102:1012–1026
- Hesse U, Schöberlein W, Wittenmayer L, Förster K, Warnstorff K, Diepenbrock W, Merbach W (2003) Effects of *Neotyphodium* endophytes on growth, reproduction and drought-stress tolerance of three *Lolium perenne* L. genotypes. *Grass Forage Sci* 58:407–415
- Higgins KL, Arnold AE, Coley P, Kursar T (2014) Communities of fungal endophyte in tropical forest grasses: highly diverse host- and habitat generalists characterized by strong spatial structure. *Fungal Ecol* 8:1–11
- Iqbal J, Nelson JA, McCulley RL (2013) Fungal endophyte presence and genotype affect plant diversity and soil-to-atmosphere trace gas fluxes. *Plant Soils* 364:15–27
- Khan AL, Hamayun M, Kang SM, Kim YH, Jung HY, Lee JH, Lee IJ (2012) Endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress: an example of *Paecilomyces formosus* LHL10. *BMC Microbiol* 12:3
- Kiers ET, Denison RF (2008) Sanctions, cooperation, and the stability of plant rhizosphere mutualisms. *Annu Rev Ecol Syst* 39:215–236
- Kiers ET, Ratcliff WC, Denison RF (2013) Single-strain inoculation may create spurious correlations between legume fitness and rhizobial fitness. *New Phytol* 198:4–6
- Kogel KH, Franken P, Huckelhoven R (2006) Endophyte or parasite - what decides? *Curr Opin Plant Biol* 9:358–363
- Kuldau G, Bacon C (2008) Clavicipitaceous endophytes: their ability to enhance resistance of grasses to multiple stresses. *Biol Control* 46: 57–71
- Kusari S, Spiteller M (2012) Are we ready for industrial production of bioactive plant secondary metabolites utilizing endophytes? *Nat Prod Rep* 28:1203–1207
- Kusari S, Zuhlke S, Spiteller M (2009) An endophytic fungus from *Camptotheca acuminata* that produces camptothecin and analogues. *J Nat Prod* 72:2–7
- Kusari S, Hertweck C, Spiteller M (2012) Chemical ecology of endophytic fungi: origins of secondary metabolites. *Chem Biol* 19:792–798
- Kusari S, Singh S, Jayabaskaran C (2014) Biotechnological potential of plant-associated endophytic fungi: hope versus hype. *Trends Biotechnol* 32:297–303
- Lahrman U, Dinga Y, Banhara A, Rath M, Hajirezaei MR, Döhlemanna S, Wirénd NV, Parniskeb M, Zuccarola A (2013) Host-related metabolic cues affect colonization strategies of a root endophyte. *Proc Natl Acad Sci* 110:13965–13970
- Lebeis SL (2014) The potential for give and take in plant–microbiome relationships. *Front Plant Sci* 5:287
- Li TY, Zeng HL, Ping Y, Lin H, Fan XL, Guo ZG, Zhang CF (2007) Construction of a stable expression vector for *Leifsonia xyli* subsp. *cynodontis* and its application in studying the effect of the bacterium as an endophytic bacterium in rice. *FEMS Microbiol Lett* 267:176–183
- Li CH, Shi L, Han Q, Hu HL, Zhao MW, Tang CM, Li SP (2012) Biocontrol of *verticillium* wilt and colonization of cotton plants by an endophytic bacterial isolate. *J Appl Microbiol* 113:641–651
- Malinowski DP, Belesky DP (2006) Ecological importance of *Neotyphodium* spp. grass endophytes in agroecosystems. *Grass Sci* 52:1–14
- Mallete ND, Knighton WB, Strobel GA, Carlson RP, Peyton BM (2012) Resolution of volatile fuel compound profiles from *Ascocoryne sarcoides*: a comparison by proton transfer reaction-mass spectrometry and solid phase microextraction gas chromatography–mass spectrometry. *AMB Express* 2:23
- Márquez LM, Redman RS, Rodriguez RJ, Roossinck MJ (2007) A virus in a fungus in a plant—three way symbiosis required for thermal tolerance. *Science* 315:513–515
- Mathys J, De-Cremer K, Timmermans P, Kerckhove SV, Lievens B, Vanhaecke M, Cammue BP, De-Coninck B (2012) Genome wide characterization of ISR induced in *Arabidopsis thaliana* by *Trichoderma hamatum*T382 against *Botrytis cinerea* infection. *Front Plant Sci* 3:108
- Mendoza AR, Sikora RA (2009) Biological control of *Radopholus similis* by co application of the mutualistic endophyte *Fusarium oxysporum* strain 162, the egg pathogen *Paecilomyces lilacinus* strain 251 and the antagonistic bacterium *Bacillus firmus*. *Bio Control* 54:263–272
- Mitter B, Petric A, Shin MW, Chain PS, Hauberg-Lotte L, Reinhold Hurek B, Nowak J, Sessitsch A (2013) Comparative genome analysis of *Burkholderia phytofirmans* PsJN reveals a wide spectrum of endophytic lifestyles based on interaction strategies with host plants. *Front Plant Sci* 4:120
- Moricca S, Ragazzi A (2008) Fungal endophytes in Mediterranean oak forests: A lesson from *Disculcaquercina*. *Phytopathology* 98:380–386
- Mostert L, Crous PW, Petrini O (2000) Endophytic fungi associated with shoots and leaves of *Vitis vinifera*, with specific reference to the *Phomopsis viticola* complex. *Sydowia* 52:46–58
- Mousa WK, Raizada MN (2013) The diversity of anti-microbial secondary metabolites produced by fungal endophytes: an interdisciplinary perspective. *Front Microbiol* 4:65
- Nagabhyru P, Dinkins RD, Wood CL, Bacon CW, Schardl CL (2013) Tall fescue endophyte effects on tolerance to water-deficit stress. *BMC Plant Biol* 13:127
- Newman LA, Reynolds CM (2005) Bacteria and phytoremediation: New uses for endophytic bacteria in plants. *Trends Biotechnol* 23:6–8
- Ownley BH, Gwinn KD, Vega FE (2010) Endophytic fungal entomopathogens with activity against plant pathogens: ecology and evolution. *Bio Control* 55:113–128
- Partida-Martínez LP, Heil M (2011) The microbe-free plant: fact or artifact? *Front Plant Sci* 2:100
- Petrini O (1991) Fungal endophytes of tree leaves. In: Andrews JH, Hirano SS (eds) *Microbial Ecology of Leaves*. Springer-Verlag, New York, USA, p 179
- Porrás-Alfaro A, Bayman P (2011) Hidden fungi, emergent properties: endophytes and microbiomes. *Annu Rev Phytopathol* 49:291–315
- Qawasmeh A, Objed HK, Raman A, Wheatley W (2012) Influence of fungal endophyte infection on phenolic content and antioxidant activity in grasses: interaction between *Lolium perenne* and different strains of *Neotyphodium lolii*. *J Agric Food Chem* 60:3381–3388
- Rasmussen S, Parsons AJ, Popay A, Xue H, Newman JA (2008) Plant-endophyte-herbivore interactions: More than just alkaloids? *Plant Signal Behav* 3:974–977
- Redecker D, Kodner R, Graham LE (2000) Glomalean Fungi from the Ordovician. *Science* 289:1920–1921
- Redman RS, Dunigan DD, Rodriguez RJ (2001) Fungal symbiosis: from mutualism to parasitism, who controls the outcome, host or invader? *New Phytol* 151:705–716
- Redman RS, Sheehan KB, Stout RG, Rodriguez RJ, Henson JM (2002) Thermotolerance conferred to plant host and fungal endophyte during mutualistic symbiosis. *Science* 298:1581

- Reinhold-Hurek B, Hurek T (2011) Living in side plants: bacterial endophytes. *Curr Opin Plant Biol* 14:435–443
- Rey T, Schornack S (2013) Interactions of beneficial and detrimental root-colonizing filamentous microbes with plant hosts. *Genome Biol* 14:121
- Riyaz-Ul-Hassan S, Strobel A, Booth E, Knighton B, Floerchinger C, Sears J (2012) Modulation of volatile organic compound formation in the Mycodiesel-producing endophyte *Hypoxylon* sp. CI-4. *Microbiology* 158:465–473
- Riyaz-Ul-Hassan S, Strobel G, Geary B, Sears J (2013) An endophytic *Nodulisporium* sp. from Central America producing volatile organic compounds with both biological and fuel potential. *J Microbiol Biotechnol* 23:29–35
- Rodriguez RJ, Roossinck M (2012) Viruses, fungi and plants: cross-kidnapping communication and mutualism. *Biocomm Fungi*. doi:10.1007/978-94-007-4264-2-14
- Rodriguez RJ, Henson J, Van Volkenburgh E, Hoy M, Wright L, Beckwith F, Kim Y, Redman RS (2008) Stress tolerance in plants via habitat-adapted symbiosis. *ISME J* 2:404–416
- Rodriguez RJ, White JF Jr, Arnold AE, Redman RS (2009) Fungal endophytes: diversity and functional roles. *New Phytol* 182:314–330
- Rosenblueth M, Martínez-Romero E (2006) Bacterial Endophytes and Their Interactions with Hosts. *Mol Plant Microbe Interact* 19:827–837
- Rudgers JA, Miller TE, Ziegler SM, Craven KD (2012) There are many ways to be a mutualist: endophyte fungus reduces plant survival but increases population growth. *Ecology* 93:565–574
- Ryan RP, Germaine K, Franks AA, Ryan DJ, Dowling DN (2008) Bacterial endophytes: recent developments and applications. *FEMS Microbiol Lett* 278:1–9
- Saikkonen K, Faeth SH, Helander M, Sullivan TJ (1998) Fungal endophytes: a continuum of interactions with host plants. *Annu Rev Ecol Syst* 29:319–343
- Saikkonen K, Wäli P, Helander M, Faeth SH (2004) Evolution of endophyte-plant symbioses. *Trends Plant Sci* 9:275–280
- Saikkonen K, Gundel PE, Helander M (2013) Chemical ecology mediated by fungal endophytes in grasses. *J Chem Ecol* 39:962–968
- Schardl CL, Liu J, White JK, Finkel RA, An Z, Siegel M (1991) Molecular phylogenetic relationship of non-pathogenic grass mycosymbionts and clavicipitaceae plant pathogens. *Plant Syst Evol* 178:27–41
- Schardl CL, Leuchtman A, Spiering MJ (2004) Symbioses of grasses with seedborne fungal endophytes. *Annu Rev Plant Biol* 55:315–340
- Scherwinski K, Grosch R, Berg G (2008) Effect of bacterial antagonists on lettuce: active biocontrol of *Rhizoctonia solani* and negligible, short-term effects on non target microorganisms. *FEMS Microbiol Ecol* 64:106–116
- Schimbock M, Lorito M, Wang ML, Hayes MK, Atac IA, Scala F, Harman GE, Kubicek CP (1994) Parallel formation and synergism of hydrolytic enzymes and peptaibol antibiotics, molecular mechanisms involved in the antagonistic action of *Trichoderma harzianum* against phytopathogenic fungi. *Appl Environ Microbiol* 4364–4370
- Schulz B, Boyle C (2005) The endophytic continuum. *Mycol Res* 109:661–687
- Selim KA, El-Beih AA, AbdEl-Rahman TM, El-Diwany A (2012) Biology of Endophytic Fungi. *Curr Res Environ Appl Mycol* 2:31–82
- Seo DJ, Nguyen DM, Song YS, Jung WJ (2012) Induction of defense response against *Rhizoctonia solani* in cucumber plants by endophytic bacterium *Bacillus thuringiensis* GS1. *J Microbiol Biotechnol* 22:407–415
- Sessitsch A, Hardoim P, Doring J, Weilharter A, Krause A, Woyke T, Mitter B, Houbert-lotte L, Friedrich F, Rahalkar M, Hurek T, Sarkar A, Bodrossy L, van Overbeek L, Brar D, van Elsas JD, Reinhold-Hurek B (2012) Functional characteristics of an endophyte community colonizing rice roots as revealed by metagenomic analysis. *Mol Plant Microbe Interact* 25:28–36
- Sherameti I, Shahollari B, Venus Y, Altschmied L, Varma A, Oelmüller R (2005) The endophytic fungus *Piriformospora indica* stimulates the expression of nitrate reductase and the starch-degrading enzyme glucan-water dikinase in tobacco and *Arabidopsis* roots through a homeodomain transcription factor which binds to a conserved motif in their promoters. *J Biol Chem* 280:26241–26247
- Sherameti I, Tripathi S, Varma A, Oelmüller R (2008) The root-colonizing endophyte *Piriformospora indica* confers drought tolerance in *Arabidopsis* by stimulating the expression of drought stress-related genes in leaves. *Mol Plant Microbe Interact* 21:799–800
- Sikora RA, ZumFelde A, Mendoza A, Menjivar R, Pocasangre L (2010) *In planta* suppressiveness to nematodes and long-term root health stability through biological enhancement - do we need a cocktail? *Acta Hort* 879:553–560
- Singh LP, Gill SG, Tuteja N (2011) Unraveling the role of fungal symbionts in plant abiotic stress tolerance. *Plant Signal Behav* 6:175–191
- Singh RK, Malik N, Singh S (2013) Improved nutrient use efficiency increases plant growth of rice with the use of IAA-overproducing strains of endophytic *Burkholderia cepacia* strain RRE25. *Microb Ecol* 66:375–384
- Soliman SSM, Trobacher CP, Tsao R, Greenwood JS, Raizada MN (2013) A fungal endophyte induces transcription of genes encoding a redundant fungicide pathway in its host plant. *BMC Plant Biol* 13:93
- Stepniewska Z, Kuzniar A (2013) Endophytic microorganisms—promising applications in bioremediation of greenhouse gases. *Appl Microbiol Biotechnol* 97:9589–9596
- Straub D, Rothballer M, Hartmann A, Ludewig U (2013) The genome of the endophytic bacterium *H. frisingense* GSF30T identifies diverse strategies in the *Herbaspirillum* genus to interact with plants. *Front Microbiol* 4:168
- Strobel G (2006) *Muscodor albus* and its biological promise. *J Ind Microbiol Biotechnol* 33:514–522
- Strobel GA (2015) Bioprospecting-fuels from fungi. *Biotechnol Lett*. doi:10.1007/s10529-015-1773-9
- Strobel G, Daisy B, Castillo U, Harper J (2004) Natural products from endophytic microorganisms. *J Nat Prod* 67:257–268
- Strobel GA, Knighton B, Kluck K, Ren Y, Livinghouse T, Griffen M, Daniel Spakowicz D, Sears J (2008) The production of myco-diesel hydrocarbons and their derivatives by the endophytic fungus *Gliocladium roseum* (NRRL 50072). *Microbiology* 154:3319–3328
- Tanaka A, Christensen MJ, Takemoto D, Park P, Scott B (2006) Reactive oxygen species play a role in regulating a fungus-perennial ryegrass mutualistic interaction. *Plant Cell* 18:1052–1066
- Tikhonovich IA, Provorov NA (2009) From plant-microbe interactions to symbiogenetics: a universal paradigm for the interspecies genetic integration. *Ann Appl Biol* 154:341–350
- Ulrich K, Ulrich A, Ewald D (2008) Diversity of endophytic bacterial communities in poplar grown under field conditions. *FEMS Microbiol Ecol* 63:169–180
- Van Bael SA, Estrada C, Rehner SA, Santos JF, Wcislo WT (2012) Leaf endophyte load influences fungal garden development in leaf-cutting ants. *BMC Ecol* 12:23
- Van der Heijden MGA, Engel RS, Riedl R, Siegrist S, Neudecker A, Ineichen, Boller KT, Wiemken A, Sanders IA (2006) The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. *New Phytol* 172:739–752
- Vandenkoomhuysse P, Baldauf SL, Leyval C, Straczek J, Young JP (2002) Extensive fungal diversity in plant roots. *Science* 295:2051
- Vega FE, Simpkins A, Aime MC, Posada F, Peterson SW, Rehner SA, Infante F, Castillo A, Arnold AE (2010) Fungal endophyte diversity in coffee plants from Colombia, Hawai'i, Mexico and Puerto Rico. *Fungal Ecol* 3:122–138

- Wade MJ (2007) The co-evolutionary genetics of ecological interactions. *Nat Rev Genet* 8:185–195
- Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, Fischer M, Heier T, Huckelhoven R, Neumann C, von Wettstein D, Franken P, Kogel KH (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proc Natl Acad Sci U S A* 102:13386–13391
- Waqas M, Khan AL, Lee IJ (2014) Bioactive chemical constituents produced by endophytes and effects on rice plant growth. *J Plant Interact* 9:478–487
- Wheatley RE (2002) The consequences of volatile organic compound mediated bacterial and fungal interactions. *Antonie Van Leeuwenhoek* 81:357–364
- White JF Jr, Torres MS (2010) Is plant endophyte-mediated defensive mutualism the result of oxidative stress protection? *Physiol Plant* 138:440–446
- Yadav V, Kumar M, Deep DK, Kumar H, Sharma R, Tripathi T, Tuteja N, Saxena AK, Johri AK (2010) A phosphate transporter from the root endophytic fungus *Piriformospora indica* plays a role in phosphate transport to the host plant. *J Biol Chem* 285:26532–26544